Pedobiologia - Journal of Soil Ecology 74 (2019) 43–53

Contents lists available at ScienceDirect

Pedobiologia - Journal of Soil Ecology

journal homepage: www.elsevier.com/locate/pedobi

Scale dependency of dispersal limitation, environmental filtering and biotic interactions determine the diversity and composition of oribatid mite communities

Huijie Gan[a,*], Donald R. Zak[a,b], Mark D. Hunter[a]

[a] University of Michigan, Department of Ecology and Evolutionary Biology, 830 N University, Ann Arbor, MI 48109, United States
[b] University of Michigan, School for Environment and Sustainability, 440 Church Street, Ann Arbor, MI 48109, United States

ARTICLE INFO

Keywords:
Body size
Community assembly
Deglaciation
Grain size
Spatial scale

ABSTRACT

It has long been established that the spatial scale of inquiry affects the ecological patterns that are revealed. However, studies of the ecological drivers underlying the assembly of soil animal communities rarely adopt a multi-scale perspective. Here, we quantified the distribution of oribatid richness along a chronosequence of temperate hardwood forests in a deglaciated region of eastern North America and analyzed variation in oribatid community structure at two grain sizes: 0.1 m^2 and 900 m^2, and two spatial extents: 20–150 m and 80–420 km. At the largest spatial scale, oribatid richness was similar among sites in the chronosequence. This suggests that oribatid mites faced minimal dispersal limitation during recolonization of deglaciated regions, likely due to long-distance passive dispersal events enabled by their small body size. However, dispersal limitation affected the community assembly at the spatial scale of 80–420 km, whereby the magnitude of dispersal limitation varied with body size and habitat type. Specifically, large-bodied mites in the litter layer experienced a stronger dispersal limitation than did small-bodied ones; and small-bodied mites were limited by dispersal in the mineral soil but not in the litter layer. Environmental filtering, particularly water content in litter and soil, played an important role in shaping oribatid mite communities at both spatial scales. In contrast, competition among oribatid species and biotic interactions with other soil microarthropods appeared to have little influence on oribatid mite community assembly, even within the smallest spatial scale. A majority of the local oribatid assemblages exhibited random coexistence patterns, with a small fraction (14%) of the assemblages exhibiting patterns of segregation consistent with competition among oribatid species. Overall, our study highlights the scale dependency of dispersal limitation during oribatid community assembly, and calls for future comparative studies to encompass a wider range of body size and habitat types.

1. Introduction

The relative role of stochastic and deterministic processes as drivers of community assembly remains an actively debated topic in ecology (Tilman, 2004; Chase, 2010; Rosindell et al., 2012). Soil animal communities, which contain an astonishing diversity, may hold promise for generating important insights into the ecological forces shaping community assembly (Giller, 1995). In particular, the high species richness of oribatid mites has attracted the attention of soil ecologists, with increasing interest in investigating the role of deterministic and stochastic drivers of oribatid mite community assembly (Lindo and Winchester, 2009; Nielsen et al., 2010; Zaitsev et al., 2012; Caruso et al., 2012; Gao et al., 2014). However, there are often contrasting results from different studies and our understanding of the ecological drivers underlying community assembly in soils remains incomplete (Maaß et al., 2015).

The spatial scales of investigation, including grain size (i.e., size of the individual units of observation) and spatial extent (i.e., overall area encompassed by a study), can affect the ecological patterns that are observed and analyzed (Wiens, 1989), and thus may prove key in understanding the contrasting results of niche vs. neutral processes among empirical studies (Cavender-Bares et al., 2006). While various processes can operate simultaneously to influence community assembly, various drivers are likely to manifest and dominate at different spatial scales (Weiher et al., 2011). In local assemblages (e.g., within one soil core), competition for resources within a functional guild could plausibly be a major driver for community assembly (Weiher and Keddy, 1995; Maaß

* Corresponding author. Current address: Horticulture Section, School of Integrative Plant Science, Cornell University, 147B Plant Science Building, 236 Tower Road, Ithaca, NY 14850, United States.
E-mail address: hg326@cornell.edu (H. Gan).

https://doi.org/10.1016/j.pedobi.2019.03.002
Received 3 June 2017; Received in revised form 27 March 2019; Accepted 29 March 2019
0031-4056/ © 2019 Elsevier GmbH. All rights reserved.

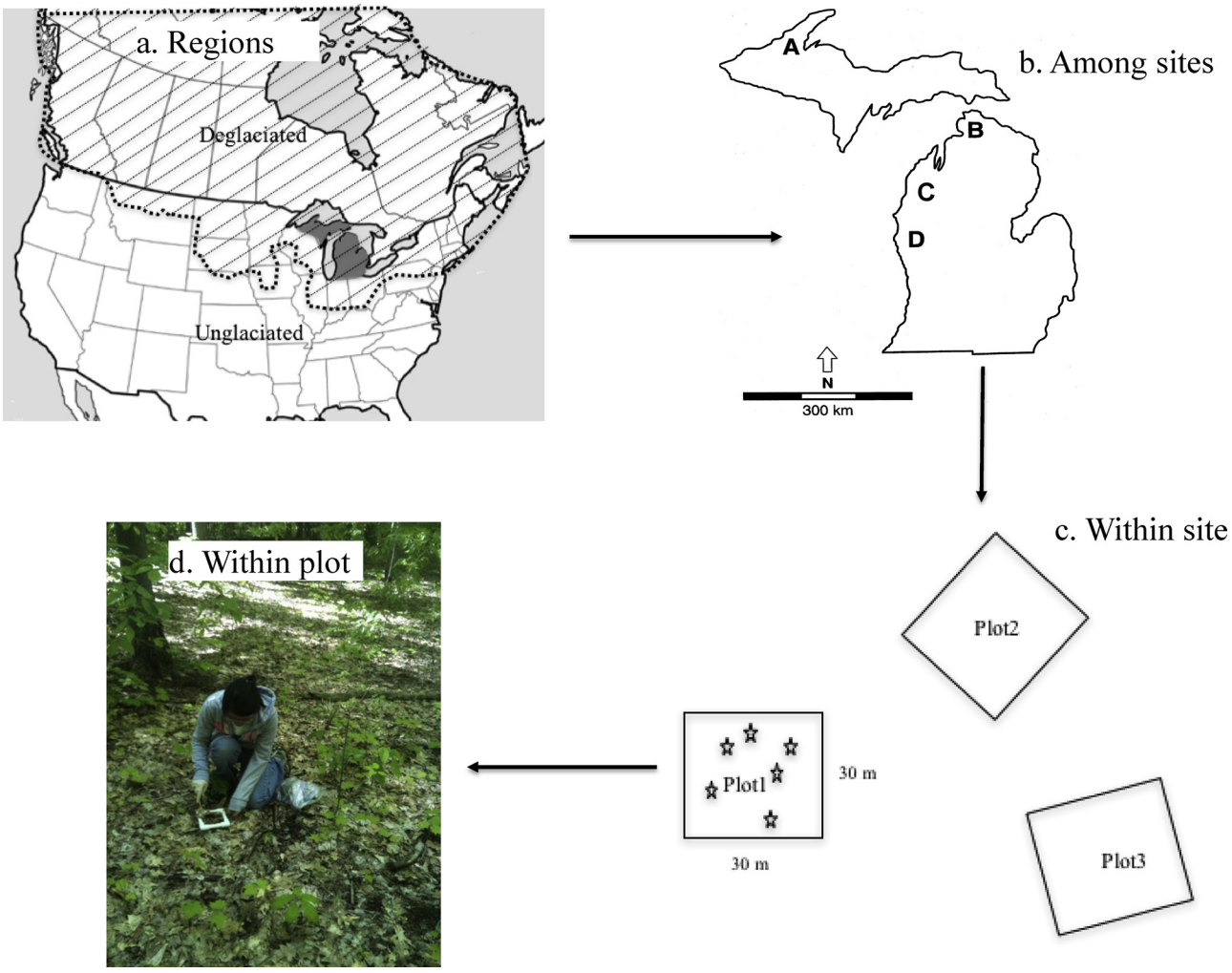

Fig. 1. Spatial scales involved in this study. a. The study sites are located in Michigan, USA (dark grey areas) in de-glaciated regions (striped areas) of North America. The dashed line depicts the maximum extent of the last glaciation, known as the Wisconsin advance, approximately 18,000 years ago (Dyke, 2004). b. Distribution of the four study sites. c. Plots within each site, with stars depicting the randomly-selected locations for sampling. d. Forest floor samples were collected within areas defined by a 10 × 10 cm PCV frame.

et al., 2015). Patterns observed at fine spatial scales (from 10 cm to 100 m) can also be governed by stochastic events such as probabilistic dispersal (Caruso et al., 2012). As the spatial scale of investigation increases to encompass more environmental heterogeneity, environmental filtering is likely to override interspecific competition and ecological drift (Geheber and Geheber, 2016). Although it has been suggested that scaling issues should be a primary focus of ecological research (Wiens, 1989; Levin, 1992), processes governing different spatial scales have not been investigated explicitly in the studies of soil community assembly.

Defining the "appropriate" scale in the study of ecological drivers of community assembly depends, in part, on the mobility and activity of organisms and their "perception" of the surrounding environment (Kraft et al., 2015). Habitat characteristics, particularly the existence of barriers and dispersal agents among suitable microhabitats, can further influence dispersal modes and dispersal rates, and thus the spatial distribution of organisms. Due to the lack of continuous inter-connectance among soil pores, soil-dwelling animals, including oribatid mites, generally exhibit low locomotive activity (Berthet, 1964), wherein the maximum active dispersal rate of oribatid mites is estimated to be 1–8 m $year^{-1}$ in forest soils (Ojala and Huhta, 2001). However, passive dispersal via water, animals, or wind can contribute to long-distance dispersal, especially for oribatid mites dwelling on the soil surface (Norton, 1980; Coulson et al., 2002; Lehmitz et al., 2011). In addition, the body size of the organisms may also influence their dispersal; for example, small-bodied organisms are easier to transport, which is likely conducive to passive dispersal (Finlay, 2002). As such, oribatid mites from different size groups and habitats may "perceive" their environment differently and generate different spatial patterns.

The degree of dispersal limitation also mediates the relative influence of contemporary environmental factors vs. historical ecological events on present-day species distribution (Martiny et al., 2006). Rapid dispersal can lessen or erase the influence of historical events, whereas community assembly of organisms with low dispersal largely reflects past ecological history (Martiny et al., 2006). For instance, the Wisconsin Glaciation eliminated most indigenous earthworms in northeastern North America (Gates, 1982; Reynolds, 2004). The majority of the earthworms now inhabiting soils in this region result from relatively new introductions of European earthworms, which began largely within the last two or three decades (Scheu and Parkinson, 1994). Compared to the systematic research that has been conducted on earthworms, the distributions and community assembly of soil oribatid mites in post-glaciation regions have rarely been investigated.

In this study, we quantified the geographic distribution of oribatid mites along a chronosequence (9500 – 13,500 years) in a glaciated region of eastern North America. We first focused on the role of historical contingency in the distribution of oribatid richness, and argue that if oribatid communities were limited by dispersal and thus were

still under range expansion following glacial retreat (similar to that of earthworms in the same region), species richness of oribatid mites would increase with time since deglaciation. Secondly, we investigated the roles of dispersal limitation, environmental filtering, and biotic interactions in the composition of oribatid communities at two grain sizes: 0.1 m^2 and 900 m^2, and two spatial extents: 20 m–150 m and 80 km–420 km. We hypothesized that competition with other functionally similar soil microarthropods, as well as competition among oribatid species, would be an important driver of oribatid community assembly at the scale of local assemblages (within 0.1 m^2), a spatial scale at which organisms are likely to interact. As grain size and spatial extent increase, we expected that environmental filtering and dispersal limitation would become important. In addition, we hypothesized that the contribution of dispersal limitation would differ among oribatid mites with different dispersal abilities. In particular, we expected that small-bodied oribatid mites living in the litter layer on the soil surface would experience a lower degree of dispersal limitation than would large-bodied mites in the mineral soil.

2. Materials and methods

2.1. Site description

Oribatid mites were sampled from four study sites spanning 420 km across Lower and Upper Michigan, USA (Fig. 1a, b). These sites are well suited to test the effect of glacial retreat on soil fauna communities, because they differ in their ages since deglaciation. We denote the four sites from north to south as site A, site B, site C and site D with ages of 9500, 11,000, 13,000 and 13,500 years, respectively (W. Farrand, *personal communication*; Farrand and Eschman, 1974).

Each site contains three 30-m x 30-m plots that are 20 to 250 m apart (Fig. 1c). All plots are sugar maple (*Acer saccharum* Marsh.) dominated northern hardwood forest, which is a prevalent natural ecosystem in northeastern North America. The overstory ages are similar among sites, ranging from 107 to 113 years (in 2019, Patterson et al., 2012), ensuring that the glacial chronosequence is not confounded by different successional stages of the sites. These hardwood forests are underlain by sandy soils that are well-drained sandy typic Haplothords of the Kalkaska series. The understory vegetation consists of mainly sugar maple seedlings (~ 90% of all stems), and the Oi horizon (i.e., litter layer) is primarily sugar maple leaf litter (Patterson et al., 2012). These plots are maintained as part of a long-term experimental study (ambient plots of The Michigan Nitrogen Gradient Study: http://webpages.uidaho.edu/nitrogen-gradient/), with plot-level environmental factors well characterized, benefiting our investigation of the environmental filtering hypothesis.

2.2. Sample collection

Plant litter that was slightly to highly decomposed on the forest floor (the O horizon, 2 ~ 5 cm thick) was sampled on three dates: May 2011, June 2012, and August 2012. On each date, we collected 6 litter samples (10 cm × 10 cm, Fig. 1d) from each plot, resulting in a total of 216 litter samples for this study (3 dates × 4 sites × 3 plots × 6 samples = 216). On the second and third sampling dates, we also collected mineral soil (top 5 cm of the A horizon) from directly underneath three of the litter samples using a 5 cm diameter soil core, resulting in a total of 72 mineral soil samples (2 dates × 4 sites × 3 plots × 3 samples = 72).

The litter and soil samples were placed inside individual plastic bags in coolers and transported to the lab within 48 h. Each sample was transferred to a modified Tullgren funnel (Crossley and Blair, 1991) to remove microarthropods over a 5-day period; extracted microarthropods were stored in 70% ethanol for sorting and identification. Three major groups (Mesostigmata, Collembola and Oribatida) of the extracted microarthropods were enumerated under a microscope. The most abundant group (Oribatida, adults only) was further identified to genus or species, based on the keys written by R. A. Norton and V. M. Behan-Pelletier (unpublished data) for use at the Ohio State University 2010 Summer Acarology Program (https://acarology.osu.edu/programs).

2.3. Biotic and abiotic factors at different grain sizes

We defined oribatid mites collected within a 10 cm × 10 cm area of the litter layer or a 5 cm × 5 cm soil core as a local oribatid mite assemblage, within which oribatid mites are likely to interact among themselves as well as with other competitors and predators. At the local assemblage level, we quantified the abundance of collembolans (potential competitors) and Mesostigmata mites (general predators). The wet and oven-dried weights of the litter were obtained to calculate the litter moisture content at the time of sampling (only available in May 2011 and June 2012).

Global positioning system (GPS) coordinates were taken at the center of each plot and the geographic distance among plots was calculated as the great circle distance based on the GPS coordinates of the plot. We calculated pairwise distances between plots within the same site (20–150 m), as well as pairwise distances between plots among different sites (80–420 km). Meanwhile, we compiled plot-level habitat factors that are known to influence the ecology of oribatid mites in the litter layer (Table 1), including annual averages of air temperature, amount of litter input, and nitrogen (N) concentration in the litter. We also included litter calcium (Ca) content in the abiotic factors because

Table 1
Environmental factors across four study sties. The values are averaged (S.D. inside parentheses) from three plots within each site. Conc., concentration; Mesostig, Mesostigmata mites; LL: the litter layer.

Variables	site A	site B	site C	site D
Abiotic				
Air temperature (°C)	5.21 (0.24)	6.38 (0.51)	7.13 (0.12)	7.69 (0.1)
Litter input (g. m^{-2}. yr^{-1})	340.2 (19.2)	369.9(9.3)	487.2 (2.2)	556.7 (27.9)
Litter Ca conc. (g. Kg^{-1})	11.64 (0.85)	15.69 (1.86)	12.83 (1.82)	14.15 (0.85)
Litter N conc. (% dried weight)	0.61 (0.05)	0.86 (0.06)	0.82 (0.02)	0.7 (0.11)
Soil temperature (°C)	7.22 (0.03)	8.07 (0.46)	8.65 (0.14)	9.09 (0.18)
Soil pH	4.55 (0.3)	4.7 (0.12)	4.41 (0.12)	4.61 (0.43)
Soil matrix potential mean (MPa)	−0.08 (0)	−0.25 (0.12)	−0.12 (0.02)	−0.24 (0.07)
Soil matrix potential minimal (MPa)	−0.56 (0.08)	−1.85 (0.5)	−1.05 (0.48)	−2.09 (0.4)
Biotic				
Mesostig LL (Individuals. g^{-1} litter)	0.68 (0.3)	0.58 (0.2)	0.64 (0.24)	0.46 (0.06)
Collembolan LL (Individuals. g^{-1} litter)	0.15 (0.01)	0.42 (0.12)	0.45 (0.34)	1.39 (1.76)
Mesostig soil (Individuals. g^{-1} soil)	0.09 (0.02)	0.05 (0.03)	0.07 (0.02)	0.07 (0.04)
Collembolan soil (Individuals. g^{-1} soil)	0.03 (0.02)	0.14 (0.17)	0.08 (0.04)	0.03 (0.03)
Microbial respiration (mmol. m^{-2}. s^{-1})	3.14 (0.26)	2.75 (0.13)	2.86 (0.07)	3.53 (0.54)

Ca is key in the integument development of some oribatid species (Norton and Behan-Pelletier, 1991).

For oribatid mites in mineral soil, soil pH, annual average of soil temperature and soil moisture (represented as soil matric potential, SMP) were compiled. We also calculated the minimal soil matrix potential from July to September, during which summer drought may occur with potential influence on oribatid mites in the forest floor (Taylor and Wolters, 2005). Oribatid mites tend to have long life cycles compared to other microarthropods, with up to 5 years of developmental time from egg to adult and up to 2 years of adult survival (Norton, 1994). Therefore, all abiotic data were averaged from 5 years of measurements (2007–2011) encompassing our sampling period; soil pH was measured in 2008 alone. These environmental factors thus represent the average conditions that oribatid mites in each plot are likely to encounter during their life cycles.

For biotic factors, we calculated the plot-level density of collembolans and mesostigmata mites (for the litter layer and mineral soil separately), which were quantified from the same samples from which we counted oribatid mites. In addition, soil respiration, measured from PVC collars inserted into the forest floor, was averaged from 2009 to 2011 and used as a proxy for plot-level microbial activity. All of the environmental data (except for collembolan and mesostigmata mite density) and the methods for their measurements are archived and publicly accessible on the web: http://webpages.uidaho.edu/nitrogen-gradient/archive.html. A brief description of the methods and the original papers that published these environmental variables are provided in Appendix A.

2.4. Data analyses

2.4.1. Local oribatid mite assemblages

In total, we collected 216 local mite communities from the litter layer over 3 sampling dates and 72 local mite communities from the minerals soil over 2 sampling dates. We first used ANOVA to investigate whether the density (total number of individuals per sample) and species richness of local oribatid assemblages vary among sampling dates, sites, plots and habitats (litter layer vs. mineral soil). Distance-based permutational Multivariate Analysis of Variance (perMANOVA) was further used to analyze the variation in species composition of the local assemblages (Anderson, 2001). For the perMANOVA, Bray-Curtis dissimilarity index was used on both abundance and presence/absence (binary) of the species matrix after the Hellinger transformation (Legendre and Gallagher, 2001).

To examine how environmental filtering and biotic interactions affect local assemblages, we focused on the litter samples collected in May 2011 and June 2012 (n = 144), for which data on microhabitat characteristics were quantified including litter dry mass (a proxy for resource availability and habitat space), moisture content of the litter, the abundance of collembolans (potential competitors of oribatid mites) and Mesostigmata mites (general predators). We calculated the Pearson's correlations (ρ) between habitat characteristics and the density and species richness of the local oribatid assemblages. We expected that oribatid density would be positively correlated with abiotic factors indicative of habitat quality, but negatively correlated with collembolans and Mesostigmata abundance due to competition and predation. We further performed redundancy analyses (RDA) to investigate the influence of biotic and abiotic factors on the species composition of the local oribatid assemblages.

To examine whether competition among oribatid species has influenced their co-existence patterns in the local assemblages, we calculated the C-score (Checkerboard score; Stone and Roberts, 1990), which is a widely-used index that measures association between species pairs. The C-score for species A and B can be calculated as: $C_{AB} = (R_A - SS)/(R_B - SS)$, where R_A (R_B) is the number of occurrence for species A (B) across all sampling unites, and SS is the number of sampling units that contain both A and B (Stone and Roberts, 1990). The C-score for a given study is the sum of C-scores from all species pairs. For communities that are dominant by competitive interactions, species are less likely to co-occur in the same assemblages, leading to a segregated distribution of oribatid species and a high C-score of the communities (Gotelli, 2000). In contrast, species can aggregate in the same communities due to environmental filtering. We used null model analyses to quantify whether species co-existence patterns deviated from the expectations of a random (stochastic) assembly process. Random oribatid assemblages were generated using an independent swap algorithm (Gotelli, 2000) that maintains the species richness of each assemblage and species occurrence frequency among assemblages. To avoid the potential for confounding temporal and spatial effects, we generated the random assemblages for each plot at each sampling date, simulating the random sampling process within each plot. A total of 36 sets of communities were produced (12 plots × 3 sampling dates), each containing 6 randomly-produced local oribatid assemblages. We did not analyze the oribatid assemblages from mineral soil due to inadequate soil sampling within each plot. Based on the C-scores from the observed and the simulated communities, the Standard Effect Size (SES) were calculated as: SES = (C-observed – C-simulated)/ (C-simulated). A SES with value near zero indicates that species are randomly assembled, whereas a SES < -2 indicates species aggregation and a SES > 2 indicates species segregation (Gotelli and McCabe, 2002).

2.4.2. Plot-level oribatid mite communities

The pooling of multiple subsamples to represent soil communities within various predefined plots is common in soil ecology research (Richter et al., 1999; Ferris and Matute, 2003). We summed oribatid mites collected from samples within each plot over the three sampling dates (12 plots in total) to represent oribatid mite communities at the grain size of 30 m × 30 m. Thus, the composite communities have homogenized some degree of spatial and temporal variation within plots and represent the average oribatid communities of each plot. As the plot-level oribatid communities and the corresponding plot-level environmental factors were averaged from multiple-year measurements, any associations between the two may reflect the long-term influences of environmental factors on oribatid mite distribution.

We separated litter and mineral soil communities for analysis, because they may exhibit different spatial patterns and also respond differently to environmental factors. Because dispersal ability is likely to differ in oribatid species with different body-sizes, we further divided the communities into two sub-groups based on their adult body lengths. For each species, the average adult body length was taken from the type species description from the literature. A histogram of the body length of all species from all four study sites (79 spp.) was generated and the midpoint (0.45 mm) was used to divide the community into two subgroups. There are 40 species in the small-bodied group with their body sizes ≤0.45 mm and 39 species in the large-bodied group with their body sizes > 0.45 mm. Each oribatid community was represented by species abundance and presence/absence matrices and was Hellinger transformed before further analyses.

To test whether oribatid mite assembly is limited by dispersal at the plot level, we first examined the relationships between the dissimilarities (Bray-Curtis index, i.e., β diversity) of oribatid mite communities and the geographic distances between plots within sites (20–250 m) and among sites (80–420 km). Partial Mantel tests were used to examine the relative importance of geographic distance and environmental dissimilarity in the variation in oribatid mite composition among plots. Plot-level environmental measurements (biotic and abiotic) were converted to a dissimilarity matrix by calculating the Euclidean distance after z-transformation. Spearman's rank correlation coefficient (ρ) was used in the partial Mantel tests and significance level was tested using a permutation method (permutation times = 999) (Legendre and Legendre, 2012).

Although the Mantel test is valid for investigating the relationship between community dissimilarity and geographic distance or

environmental dissimilarity, it usually underestimates the variance partitioned by explanatory factors (Legendre et al., 2005). We therefore used redundancy analysis (RDA) to further partition the variation in original community composition (rather than the dissimilarity matrix as in the Mantel test) into spatial fraction, environmental fraction, and the spatially structured environmental fraction (Legendre et al., 2005). We first used distance-based Moran's eigenvector mapping (MEMs, also known as PCNM-principal coordinates of neighbor matrices) to generate spatial vectors based on the geographic distance matrix among plots (threshold distance = 420 km) (Dray et al., 2006). Any eigenvectors with significant positive Moran's I were used as explanatory spatial factors for the variation partitioning. To remove collinearity among environmental factors, we applied principle component analysis (PCA) to all environmental variables and then used the resulting PCA axes to represent the explanatory environmental factors for the variation partitioning. The significance of each source of variation (spatial or environmental) was tested with a Monte Carlo permutation test (permutation times = 999). In addition, we used a forward selection approach to identify the explanatory factors (including environmental and spatial factors) that contribute the most in explaining the variation in oribatid mite assembly (Blanchet et al., 2008).

2.4.3. Historical contingency in the distribution of oribatid richness at the regional scale

To investigate whether the species richness of oribatid mites varied across the glacial chronosequence, rarefaction curves were generated from the raw abundance data, with 9 data points (3 plots x 3 sampling dates) for each site (forest floor and soil combined). Ninety-five % confidence intervals were calculated for each rarefaction curve to assess any overlap among sites. It should be noted that, because some oribatid mites can only be identified to genus, the species rarefaction curves may underestimate overall species richness. To further explore how glaciation influenced present-day oribatid mite species distribution in North America, we analyzed the Catalogue of Oribatida (Acari) of the Continental United States and Canada (Marshall et al., 1987) and counted the number of oribatid species recorded in glaciated areas (Northeastern states of USA and most provinces of Canada) and the number recorded in unglaciated regions of North America (Fig. 1).

Species rarefaction curves were generated using *EstimateS* (Colwell, 2006). All other statistical analyses were conducted in R 3.3.1 (R Core Team, 2016). C-scores and null model analyses were performed in the package *EcoSimR* (Gotelli et al., 2015). perMANOVA, RDA, Mantel tests, and PCA were performed in the package *vegan* (Oksanen et al., 2007); calculation of MEMs spatial vectors and forward selection of explanatory factors were conducted in the package *adespatial* (Dray et al., 2016).

3. Results

3.1. Local oribatid mite assemblages

Overall, we collected and examined 11,101 adult oribatid mites from 79 species with 8 singletons. The density, species richness and species composition of local oribatid assemblages differed between litter layer and mineral soil, and varied among sites, plots and sampling dates (Table 2). The variation in local mite assemblages was highly correlated with variation in habitat characteristics (Table 3). In the litter layer, oribatid density ($\rho = 0.55$, $P < 0.001$) and richness ($\rho = 0.59$, $P < 0.001$) were both positively correlated with moisture content of the plant litter (Table 3). The moisture content further explained a low but significant fraction (4%, $P = 0.001$) of variation in the species composition of local oribatid assemblages (Table 3). In comparison, the amount of litter (within 10 cm × 10 cm area) did not seem to affect the local oribatid assemblages.

Contrary to our expectations, oribatid densities were positively associated with the abundance of the collembolans ($\rho = 0.38$, $P < 0.001$) and Mesostigmata mites ($\rho = 0.52$, $P < 0.001$). The degree of the correlations declined after controlling for their covariance with litter moisture but remained statistically significant ($P < 0.02$). Similarly, species richness of oribatid mites was positively correlated with the abundance of collembolans and Mesostigmata mites; however, these positive correlations disappeared after controlling for their covariance with moisture content. In addition, collembolan abundance explained a small fraction ($R^2 = 0.02$, $P < 0.05$) of variation in the species composition of local oribatid assemblages after controlling for the covariance with moisture content (Table 3). Variation in Mesostigmata mite abundance was unrelated to variation in oribatid mite community composition after removing covariance with litter moisture ($P > 0.31$).

Among the 36 sets of oribatid communities in the forest floors (12 plots x 3 sampling dates), a majority of them (86%) exhibited random patterns of oribatid species coexistence within plots (Fig. 2). Oribatid species in a small fraction (14%) of the communities co-occurred less frequently (i.e., segregated) than that expected in randomly-generated communities.

3.2. Dispersal limitation and habitat filtering for plot-level oribatid mite communities

Analyses of plot-level species composition using abundance and presence/absence matrices in general yield identical trends with varying significance levels. For the purpose of brevity, we focus on the results derived from the abundance data set in this section; results from the presence/absence data are not shown unless indicated otherwise.

Overall, the patterns of the dissimilarity-distance relationships varied depending on the spatial scales (within sites vs. among sites) of the analyses, the body size categories (small-bodied vs. large-bodied) of the oribatid mites, and their habitat associations (litter vs. mineral soil). For small-bodied mites inhabiting the litter layer, the dissimilarity/distance relationships were not significant at either the small (within sites) or the large (among sites) spatial scales (Fig. 3a, c, $P > 0.10$). In comparison, large-bodied mites in the litter layer exhibited positive dissimilarity/distance relationships at the small scale (presence/absence data only, Fig. 3b, $P = 0.03$) as well as the large spatial scale (Fig. 3c, d, $P < 0.001$ for both abundance and presence/absence data).

Oribatid mites dwelling in the mineral soil did not exhibit any significant dissimilarity/distance relationships at the small spatial scale (Fig. 4a, b, $P > 0.10$). At the large spatial scale, the dissimilarity-distance relationship was significant for small-bodied mites (Fig. 4c, d, $P = 0.042$, and $P = 0.004$ for the abundance and the presence/absence data respectively). In contrast, the dissimilarity-distance relationships for large-bodied mites in the mineral soil were not significant at the spatial scale of 80–420 km (Fig. 4c, d, $P > 0.10$). However, the dissimilarity indices for communities of large-bodied mites were significantly higher than were those of the small-bodied mites (Fig. 4c, d, students' t-test, $P < 0.001$), indicating that large-bodied oribatid communities in mineral soil may have experienced a stronger degree of isolation than small-bodied communities.

Partial Mantel tests, including both within- and among-site variation, revealed that the positive dissimilarity/distance relationships for large-bodied mites in litter, as well as for the small-bodied mites in the mineral soil, were still significant after controlling for the differences in environmental factors among plots (Table 4).

The first three PCA axes of all environmental factors accounted for > 75% of total variation (Appendix A, Fig A1) and were used to represent the environmental variables in the variation partitioning analysis. Distance-based Moran's eigenvector mapping produced one significant spatial vector, reflecting largely the spatial distribution of plots among sites. Similar to the results from analyses of the dissimilarity/distance relationships, partial RDA revealed that the spatial vector contributed significantly in determining the composition of

Table 2
Variation in oribatid density, species richness and species composition of local oribatid mite assemblages (n = 288) among sites, plots within sites, sampling dates and habitats (litter layer vs. mineral soil). *P*-values smaller than 0.05 are indicated in bold.

Factor	df	Density		Species richness		Community composition			
						Abundance		Presence/absence	
		R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*
Site	3	0.07	< **0.001**	0.22	< **0.001**	0.16	< **0.001**	0.21	< **0.001**
Plot	8	0.05	0.10	0.06	**0.03**	0.07	< **0.001**	0.07	< **0.001**
Date	2	0.05	< **0.001**	0.08	< **0.001**	0.05	< **0.001**	0.06	< **0.001**
Habitat	1	0.02	**0.03**	0.01	**0.05**	0.12	< **0.001**	0.10	< **0.001**
Residuals	265	0.81		0.63		0.60		0.56	

large-bodied mites in the litter layer (Fig. 5a, $R^2 = 0.17$, $P = 0.03$), but not in mineral soil (Fig. 5c, $P > 0.10$). For small-bodied mites, the contribution of the spatial vector was only significant in mineral soil (Fig. 5d, $R^2 = 0.09$, $P = 0.04$), but not in the litter layer (Fig. 5b, $P > 0.10$).

Environmental variables (the first 3 PCA axes) also accounted for considerable amounts of variation (19–27%, pure environmental fraction and spatially-structured environmental fraction combined) in oribatid composition (Fig. 5a,b,d; $P < 0.05$), with the exception for large-bodied mites in mineral soil (Fig. 5c, $P > 0.10$). Forward selection of each explanatory factor in spatially explicit RDA models (all mites included) further revealed that aboveground litter production (25%) and minimal summer soil moisture (9%) accounted for considerable amounts of variation in the relative abundance of oribatid mites in the litter layer (Table 5). In mineral soil, annual average of soil moisture (12%) and soil pH (6%) explained significant fractions of variation in the relative abundance of oribatid mites. The same environmental factors were selected in the RDA models with presence/abundance data (data not shown). In addition, biotic factors including collembolan and Mesostigmata density in litter and mineral soil were not significant in any of the models ($P > 0.10$).

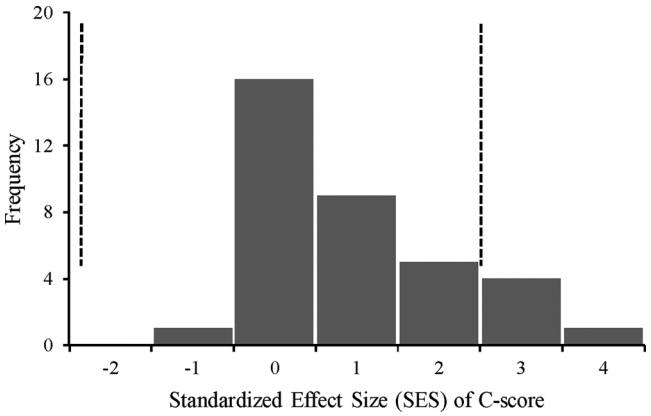

Fig. 2. Frequency histograms for Standardized Effect Size (SES) of C scores of local oribatid assemblages (n = 36) in the forest floor within plots. SES between −2.0 and 2.0 (enclosed by the dashed lines) indicate that the species coexistence patterns do not deviate from random processes; and SES > 2 indicate a segregated distribution of oribatid species among local assemblages (Gotelli and McCabe, 2002).

3.3. Distribution of oribatid richness in deglaciated regions

In contrast to our expectation, the species richness of oribatid mites did not decline northward as sites decreased in time since deglaciation; instead, the total number of oribatid species at each site was similar, ranging from 46 (Site C) to 56 (Site B and Site D). The saturation of the rarefaction curves (Fig. 6a) illustrates that we had sampled sufficiently to estimate total species richness at each of our study sites. While site D had much lower oribatid abundance than the other sites, its species richness (56 spp.) was comparable to other sites (Fig. 6a). The overlap of the 95% confidence intervals of the rarefaction curves (not shown) indicated that there was no significant difference in species richness among the four study sites. Among the 5 most dominant species at each site, three species were shared including *Scheloribates pallidulus* (17.2% to 27.4%, relative abundance), *Oppiella nova* (9.5% to16.0%) and *Suctobelbella* sp2 (7.5% to 16.5%). However, some species, such as *Eueremaeus nemoralis*, was abundant at one site (8.1% at site C), but rare at others (0.1% at sites A and B). All species information including their density in different study sites and sampling layers is provided in Appendix A Table A1.

A total of 1136 species are recorded in the Catalogue of Oribatida (Acari) of Continental United States and Canada (Marshall et al., 1987); 642 of these species occur in deglaciated areas (Northeast of USA and most parts of Canada) whereas 872 species are recorded in unglaciated regions of the southern part of North America. In addition, there are 261 species that occur only in deglaciated areas, whereas 491 species

Table 3
The associations between environmental factors and local oribatid mite assemblages of the litter layer collected in May 2011 and June 2012 (n = 144). Pearson's correlation coefficient (ρ) was used to test the correlations between oribatid density and species richness and explanatory factors. Redundancy analyses (RDA) were performed on species composition data after Hellinger transformation. *P*-values smaller than 0.05 are indicated in bold.

Environmental factors	Density		Species richness		Community composition			
					Abundance		Binary	
	ρ	*P*	ρ	*P*	R^2	*P*	R^2	*P*
Moisture content	0.55	< **0.001**	0.59	< **0.001**	0.04	**0.001**	0.04	**0.001**
Litter dry weight	0.10	0.24	−0.03	0.74	0.02	0.31	0.02	0.29
Collembolan abundance	0.38	< **0.001**	0.31	< **0.001**	0.02	**0.04**	0.03	**0.001**
Mesostigmata abundance	0.52	< **0.001**	0.41	< **0.001**	0.02	0.08	0.02	**0.01**
Collembolans| Moisture*	0.20	**0.02**	0.08	0.36	0.02	**0.04**	0.02	**0.03**
Mesostigmatas| Moisture	0.33	< **0.001**	0.14	0.09	0.01	0.37	0.01	0.31

* Partial correlation or partial RDA controlling for the variation in litter moisture content.

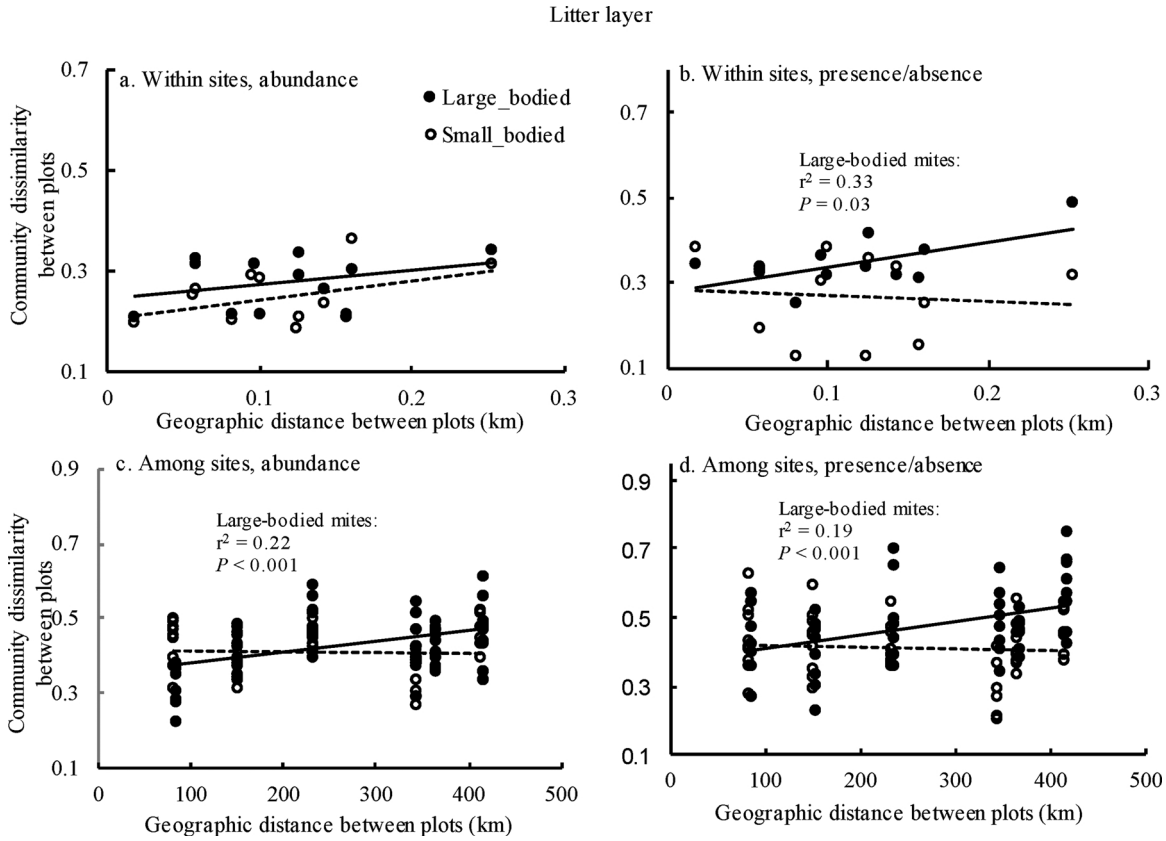

Fig. 3. Community dissimilarity-geographic distance relationships for plot-level oribatid communities for abundance (a, c) and presence/absence (b, d) data within the same sites (a, b) and between different sites (c, d) in the litter layer. Bray-Curtis dissimilarity index was calculated separately for large-bodied mite communities (solid circles and solid lines) and small-bodied mite communities (hollow circles and dashed lines) for the abundance data after Hellinger transformation. The coefficient of determination (r^2) and *P* values are shown when the slopes of the regression lines are statistically different from zero at $P < 0.05$.

are restricted to unglaciated regions (Fig. 6b).

4. Discussion

4.1. Dispersal limitation in the distribution and community assembly of oribatid mites

Overall, our results reveal that whether dispersal limitation affects the distribution and community assembly of oribatid mites is contingent on the scale of the investigation. The temporal and spatial extent at which dispersal limitation manifests is closely linked to the dispersal ability of the organisms being considered, which, in turn, can be influenced by body size and habitat characteristics. For example, unlike soil macro-fauna such as earthworms (Gates, 1982; Reynolds, 2004), we found little evidence to suggest that oribatid mites have been dispersal limited during their re-colonization following the last glacial retreat. Our data suggest that species richness was comparable among sites that vary 4000 years in the length of time since they were ice free, consistent with the large species pool of oribatids reported from glaciated regions in the Catalogue of Oribatida (Acari) of the Continental United States and Canada (Marshall et al., 1987). However, we note that recolonization by oribatid species of even our youngest site has been ongoing for the last 9500 years. The lack of dispersal limitation at this time scale does not exclude the possibility of dispersal limitation at shorter time scales. For instance, Zaitsev et al. (2012) observed that sites with geological ages < 1000 years had significantly lower oribatid species richness than did sites of > 10,000 years. Nevertheless, the small body size of oribatid mites may have increased the likelihood of long-distance dispersal events, such as dispersal by wind, drift ice/wood, or hitching on birds and other larger organisms (Norton, 1980; Coulson et al., 2002; Lebedeva and Krivolutsky, 2003; Lehmitz et al., 2011). The existence of such long-distance dispersal is likely to have enabled the relatively rapid colonization by oribatid mites across this region as compared to earthworms, which are at the other extreme of body size among soil fauna. It will be interesting to investigate how dispersal limitation influences the distribution of other groups of soil fauna with intermediate body size (e.g., Isopoda and Enchytraeidae) in deglaciated regions. Phylogenetic analyses combined with chronosequence studies could illuminate possible dispersal routes and the existence of any refugia (Rosenberger et al., 2013).

A similar pattern of dispersal advantage for small-bodied animals has been found in land snails on the Pacific islands, in which small snail genera compose 67% of Pacific island snail fauna; in contrast, only 27% of continental snail fauna are composed of small-sized taxa (Vagvolgyi, 1975). This provides indirect evidence that species with small body size may experience less limitation during aerial oversea dispersal. Small-bodied organisms are not only easier to transport, but they also generally exhibit larger population sizes that may increase the probability of dispersal (Van der Gucht et al., 2007). It has even been suggested that there exists a threshold value of body size (1 mm) under which species are ubiquitous dispersers and less likely to be geographically restricted (Finlay, 2002). Adult body lengths in oribatid mites encompass this threshold, ranging from about 0.15 mm to more than 2.00 mm, with most species not exceeding 1 mm. However, it would be unrealistic to conclude that oribatid mites are not dispersal limited solely based on their small body size, as many species (small and large) do not reach the high local densities that are required for ubiquitous dispersal. On the other hand, some oribatid mite groups can reproduce asexually (Norton, 1994), which should increase the probability of population establishment after dispersal (Hörandl, 2006). About 39% of

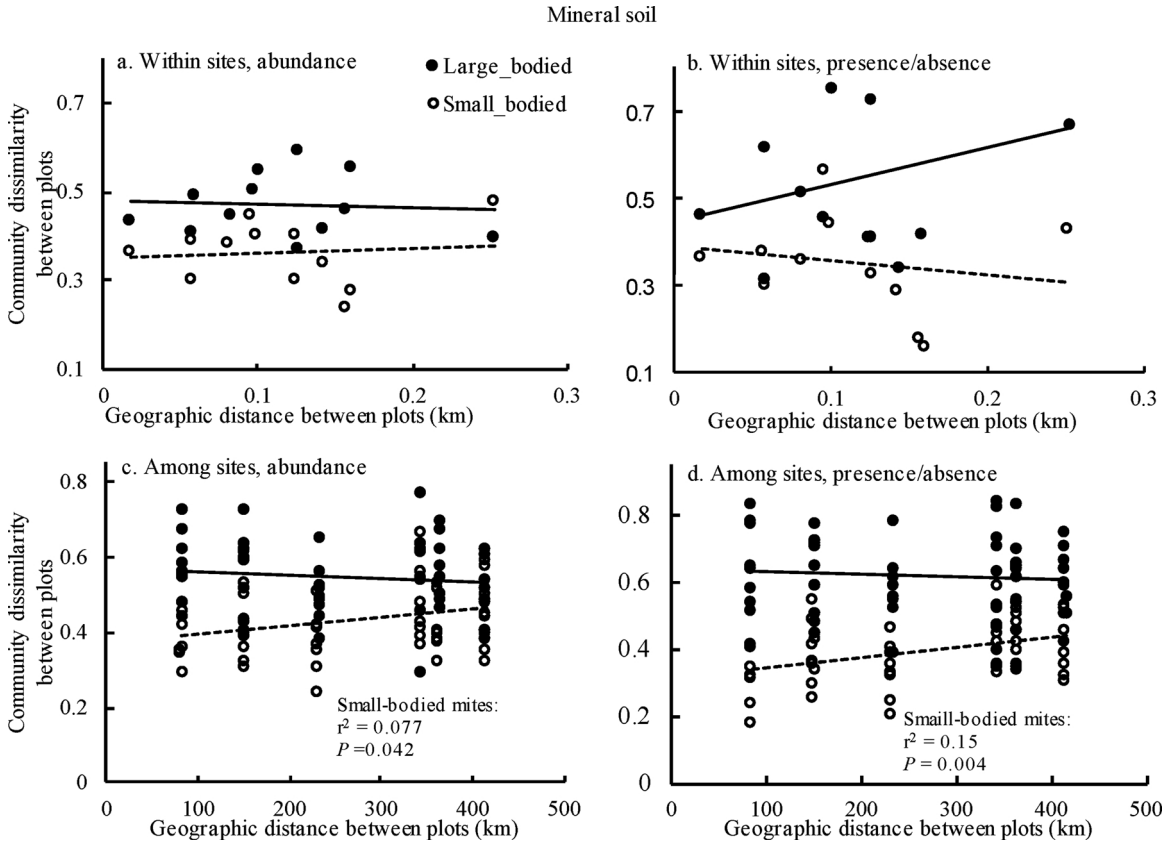

Fig. 4. Community dissimilarity-geographic distance relationships for plot-level oribatid communities for abundance (a, c) and presence/absence (b, d) data within the same sites (a, b) and between different sites (c, d) in the mineral soil. Bray-Curtis dissimilarity index was calculated separately for large-bodied mite communities (solid circles and solid lines) and small-bodied mite communities (hollow circles and dashed lines) for the presence/absence data after Hellinger transformation. The coefficient of determination (r^2) and *P* values are shown when the slopes of the regression lines are statistically different from zero at $P < 0.05$.

Table 4
Partial Mantel tests of dissimilarities of plot-level oribatid communities (n = 12) in relationship to geographic distance between plots. Partial correlation coefficients (ρ) for the relationships were calculated after controlling for the covariance of environmental dissimilarities between plots. *P*-values smaller than 0.05 are indicated in bold.

Oribatid communities	ρ	*P*
Litter layer		
Large-bodied	0.52	**0.001**
Small-bodied	0.05	0.33
All mites	0.37	**0.009**
Mineral soil		
Large-bodied	−0.04	0.58
Small-bodied	0.28	**0.04**
All mites	0.23	0.09

the 79 oribatid species in our study are parthenogenetic species (asexual reproduction). The ratio of parthenogenetic species did not differ among the four study sites and is comparable to oribatid communities reported in other forest soils (Maraun et al., 2012). High rates of passive dispersal due to small body size, combined with high population growth from asexual reproduction, likely contribute to the observed high species richness of oribatid mites across our study sites.

Although we found little evidence of dispersal limitation in the distribution of oribatid richness along this glacial chronosequence, dispersal limitation appeared to play an important role in influencing the community structure of oribatid mites in this region. However, the spatial scale at which dispersal limitation manifested differed depending on the body size and the habitat association of the mite communities. Specifically, large-bodied mites from the litter layer exhibited strong community dissimilarity/geographic distance relationships at the spatial scale of 80–420 km. The lack of such spatial pattern for small-bodied mites from the same litter layer further supports the idea that small-bodied organisms are less likely to experience dispersal limitation under similar conditions. However, there was evidence of dispersal limitation for the same small-bodied group dwelling in mineral soils, probably due to a lower likelihood of exposure to dispersal agents (animals, winds, water etc.) for species living underground (Lehmitz et al., 2011). While we expected that large-bodied mites would demonstrate a stronger dispersal limitation in mineral soil, it appeared that the isolation of large-bodied oribatid communities in mineral soil may have reached a maximum that resulted in a plateau in their dissimilarity-distance relationship at the spatial scale of 80–420 km; irrespective of distance, their communities were always less similar to one another than were those of small-bodied mites in mineral soil. Consequently, a smaller spatial scale (< 80 km) may be needed to detect the dispersal limitation for large-bodied mites in mineral soil. It should be noted that since we only sampled the top 5 cm of the mineral soil, mites dwelling in this layer may still be exposed to passive dispersal through their vertical movements to the soil surface. Future studies that explicitly compare the spatial patterns of species that show high fidelity in their microhabitat associations (Gao et al., 2018), such as surface dwellers vs. species living in deep soil, could improve our understanding of the relationships between habitat characteristics and dispersal limitation in oribatid mite communities.

Our results suggest that differences in the spatial scales of investigation, and in habitat characteristics, may help to explain conflicting results in previous studies that have examined the spatial patterns of oribatid communities (Lindo and Winchester, 2008, 2009; Caruso et al., 2012; Ingimarsdottir et al., 2012). For instance, species

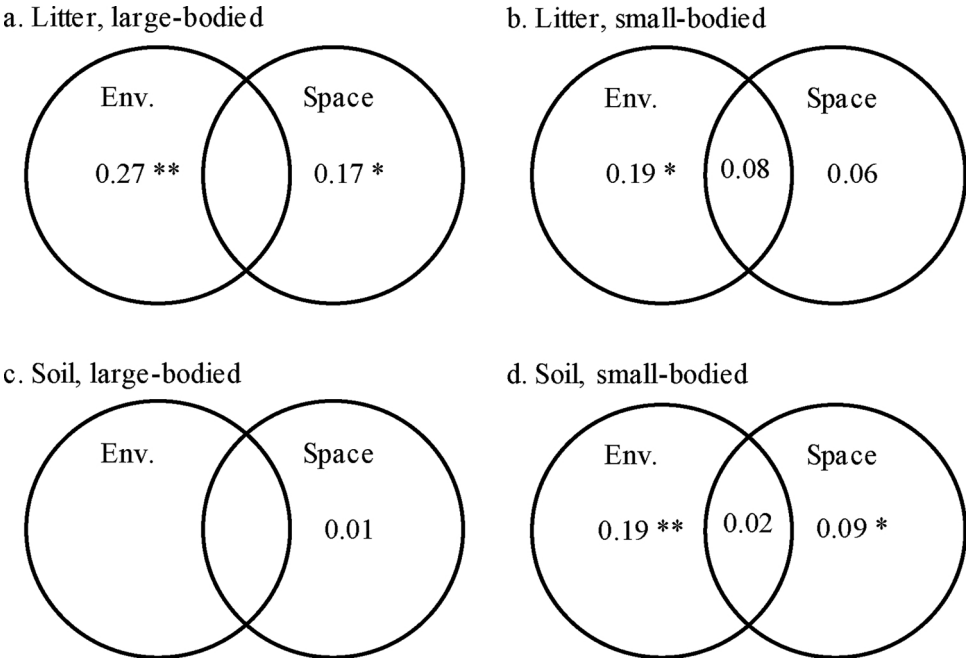

Fig. 5. Variation in plot-level oribatid communities from the litter layer (a, b) and the mineral soil (c, d) explained by environmental (Env.) factors, spatial factors and shared fractions (values in the overlapping areas) based on partial redundancy analysis (pRDA). **P < 0.01, * P < 0.05.

composition of oribatid mites in mangrove forests is affected more by microhabitat diversity than geographic distance between islands over 470 km apart (Karasawa and Hijii, 2004), because oribatid mites can disperse directly in sea water between mangrove forests (Coulson et al., 2002). In comparison, there is evidence of dispersal limitation for oribatid mites in forest soils at spatial scales spanning from 500 m (Caruso et al., 2012) to 56 km (Lindo and Winchester, 2009). Gao et al. (2014) reported that oribatid mites from the top 10 cm of soil surface are spatially structured within a spatial scale of 5 m. In contrast, we found little evidence of dispersal limitation in structuring oribatid assemblages within the spatial scale of 20–250 m (except for the presence/absence of large-bodied mites from the litter layer). High species turnover and community heterogeneity can occur at a small spatial scale due to intraspecific aggregation or species-specific microhabitat associations, and any dispersal limitation observed at this scale is likely to be confounded by unmeasured fine-scale environmental variables that are spatially structured (Dray et al., 2006). We suggest that future studies encompassing a wide range of spatial scales are needed to identify the spatial scale at which dispersal limitation is most relevant in structuring oribatid mite community assemblages.

4.2. Environmental filtering and biotic interactions as drivers of oribatid community assembly

Our results reveal that environmental filtering functions to structure oribatid communities at multiple spatial scales. At the plot level, foliar litter input and minimal soil moisture during summer significantly shaped community composition in the litter layer (34% of variance explained). In the mineral soil, both soil moisture and pH were important factors influencing the composition of oribatid mites in the mineral soil (19% of variance explained). All of these ecological factors have all been reported previously to influence oribatid communities. For example, aboveground litter input can have differential impacts on oribatid species, based on their requirements for detritus and habitat space (Irmler, 2006). Likewise, habitat moisture level is an important environmental filter for oribatid mites in canopy-suspended soils and on the forest floor (Lindo and Winchester, 2008), likely due to the wide range of sensitivity among oribatid species to desiccation (Siepel, 1996). However, our observed association between soil pH and oribatid communities is likely indirect, due to potential covariance between pH and other relevant factors such as soil microbial communities (Van Straalen and Verhoef, 1997; Nielsen et al., 2010; Gao et al., 2014). We note that our study confirms the general importance of moisture and drought in shaping oribatid communities in forest litter and soil. A single summer drought can significantly alter oribatid composition in the following year (Taylor and Wolters, 2005). As global climate change is likely to alter summer drought frequency, these findings suggest that oribatid communities in the forest floor are likely to be influenced by future climate change.

There is also increasing evidence that oribatid mite distributions are sensitive to habitat heterogeneity at small spatial scales (< 100 m) (Nielsen et al., 2010; Gao et al., 2016). Different microhabitats in the forest floor, such as litter, dead woods, lichens etc., provide variable habitat quality to oribatid mites (Wehner et al., 2016). Our study provides further evidence that even within relatively homogeneous plant litter in the forest floor, the abundance, species richness and composition of oribatid mites varies substantially with litter moisture content. This corroborates the plot-level findings that habitat moisture is the

Table 5
Forward selection of explanatory factors with significant contribution ($P < 0.05$) to explaining the variation in plot-level oribatid communities. Values inside parentheses are the proportion of total variation explained by the explanatory factors. SMP, soil matric potential.

Oribatid communities	Sequential addition of environmental factors and adjusted R^2
Litter layer	Litter input (0.25), Spatial factor (0.12), Summer minimal SMP (0.09)
Mineral soil	Annual mean SMP (0.12), Soil pH (0.07), Spatial factor (0.06)

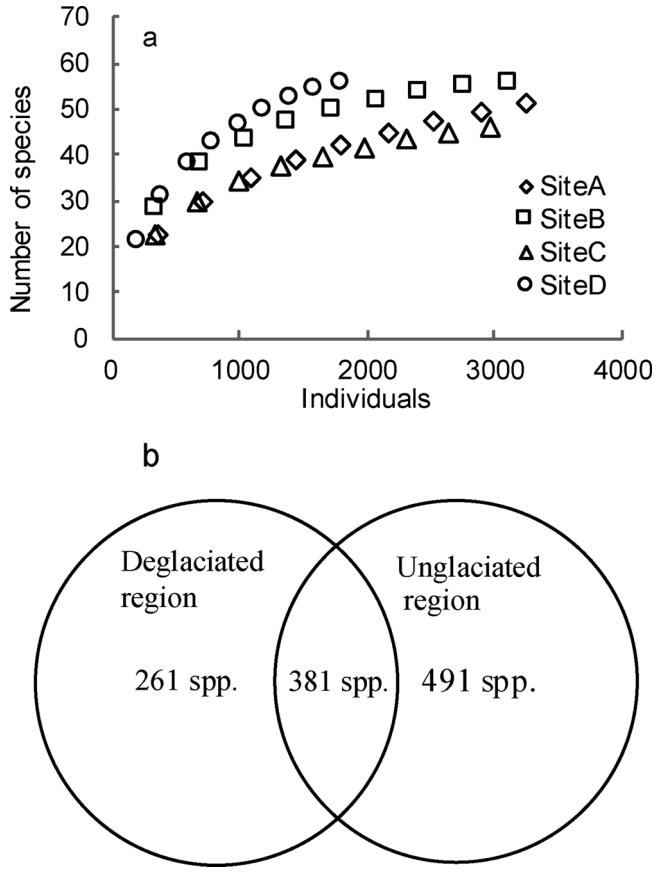

Fig. 6. Oribatid species richness in (a) the chronosequence of our four study sites illustrated through rarefaction analysis, and (b) the deglaciated and unglaciated regions of North.
America based on analysis of the Catalogue of Oribatida (Acari) of Continental United States and Canada (Marshall et al., 1987).

predominant environmental factor determining oribatid distribution at the soil surface.

In contrast to our predictions, biotic interactions appeared to have little effect on structuring oribatid mite communities at either the plot level or the local assemblage level. The coexistence patterns of oribatid species in a majority of the local oribatid communities were indistinguishable from random, suggesting that competition among oribatid mites may not drive community assembly. This is consistent with recent findings that resource-based niche partitioning and interspecific competition play a minor role in influencing oribatid communities at small scales (Maaß et al., 2015; Gao et al., 2016). As many oribatid species and Collembola rely at least partially on fungal hyphae as a food resource (Siepel and Ruiter-Dijkman, 1993; Maraun et al., 2003), competition from Collembola may alter the relative abundance of oribatid species with similar diets. However, the positive correlations between oribatid density, species richness and collembolan abundance suggest that these two functionally-similar groups are likely to prefer similar microhabitats (e.g., moist litter) rather than displacing each other. The positive relationship between oribatid density and collembolan abundance remained significant after controlling for their covariance with moisture, suggesting that other factors such as food quality in the microhabitats may act as further environmental filters for both groups of microarthropods (Mitchell et al., 2016).

While Lindo and Winchester (2009) reported a significant effect of Mesostigmata abundance on oribatid mite community composition, we did not find any evidence to suggest that Mesostigmata are an important structuring force in oribatid mite communities at either spatial scale. Many oribatid species are known to be well defended from their predators including Mesostigmata mites (Schneider and Maraun, 2009; Brückner et al., 2017). The positive correlation between oribatid density and Mesostigmata abundance in the same local assemblages indicates that oribatid mite assemblages in our study were driven mostly by bottom-up forces such as habitat quality and food availability rather than predator control (Nielsen et al., 2008; Saitoh et al., 2011).

Overall, our findings reveal that biotic interactions exert a substantial ecological force while environmental filtering (especially habitat moisture) remains a fundamental driver of soil oribatid community assembly in this temperate forest ecosystem. We are aware that the use of variation partitioning in detecting environmental filtering is limited by measuring *all* relevant environmental factors, often leading to little variation (< 5%) explained by environmental factors in similar studies (Caruso et al., 2012, 2013; Gao et al., 2014). Our study benefits from the detailed characterization of environmental variables for each plot in these long-term study sites. In addition, lagged responses to temporal fluctuations in environmental factors are common among oribatid species (Taylor and Wolters, 2005); therefore, multiple samplings may be necessary to reduce confounding effects of temporal variation in oribatid communities to facilitate the detection of environmental filtering.

Acknowledgements

Kurt Pregitzer and Andrew Burton contributed substantially to our work through their long-term dedication to the design and maintenance of the study sites, as part of a long-term field-based N deposition experiment. We thank Catherine Doktycz and Liane Racelis for their help with fieldwork. We also thank the two anonymous reviewers who helped to improve the quality of the paper. This research was supported by an EEB block grant from the University of Michigan. The study sites were maintained with grants from the National Science Foundation and the Office of Science (BER), U.S. Department of Energy.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pedobi.2019.03.002.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.
Berthet, P.L., 1964. Field study of the mobility of Oribatei (Acari), using radioactive tagging. J. Animal Ecol. 33, 443–449.
Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89, 2623–2632.
Brückner, A., Raspotnig, G., Wehner, K., Meusinger, R., Norton, R.A., Heethoff, M., 2017. Storage and release of hydrogen cyanide in a chelicerate (*Oribatula tibialis*). PANS 114, 3469–3472.
Caruso, T., Taormina, M., Migliorini, M., 2012. Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. J Anim. Ecol. 81, 214–221.
Caruso, T., Trokhymets, V., Bargagli, R., Convey, P., 2013. Biotic interactions as a structuring force in soil communities: evidence from the micro-arthropods of an Antarctic moss model system. Oecologia 172, 495–503.
Cavender-Bares, J., Keen, A., Miles, B., 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87, 109–122.
Chase, J.M., 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328, 1388–1391.
Colwell, R.K., 2006. EstimateS: Statistical Estimation of Species Richness and Shared Species From Samples, Version 8.0. http://purl.oclc.org/estimates.
Coulson, S.J., Hodkinson, I.D., Webb, N.R., Harrison, J.A., 2002. Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. Funct. Ecol. 16, 353–356.
Crossley, D.A., Blair, J.M., 1991. A high-efficiency, low-technology Tullgren-type extractor for soil microarthropods. Agric. Ecosyst. Environ. Appl. Soil Ecol. 34, 187–192.
Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model. 196, 483–493.
Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Wagner, H.H., 2016. Adespatial: Multivariate Multiscale Spatial Analysis. R Package

Version 0.0-4.
Dyke, A.S., 2004. An outline of the deglaciation of North America with emphasis on central and northern Canada. Quat. Glaciat. Chronol. Part II North Am 2b, 373–424.
Farrand, W.R., Eschman, D.F., 1974. Glaciation of the southern peninsula of Michigan: a review. Mich. Acad. 7, 31–56.
Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Agric., Ecosyst. Environ. Appl. Soil Ecol. 23, 93–110.
Finlay, B.J., 2002. Global dispersal of free-living microbial eukaryote species. Science 296, 1061–1063.
Gao, M., He, P., Zhang, X., Liu, D., Wu, D., 2014. Relative roles of spatial factors, environmental filtering and biotic interactions in fine-scale structuring of a soil mite community. Soil Biol. Biochem. 79, 68–77.
Gao, M., Liu, D., Lin, L., Wu, D., 2016. The small-scale structure of a soil mite metacommunity. Eur. J. Soil Biol. 74, 69–75.
Gao, M., Sun, X., Qiao, Z., Hou, H., Lu, T., Wu, D., Jin, G., 2018. Distinct patterns suggest that assembly processes differ for dominant arthropods in above-ground and below-ground ecosystems. Pedobiologia 69, 17–28.
Gates, G.E., 1982. Farewell to north American megadriles. Megadrilogica 4, 12–77.
Geheber, A.D., Geheber, P.K., 2016. The effect of spatial scale on relative influences of assembly processes in temperate stream fish assemblages. Ecology 97, 2691–2704.
Giller, P.S., 1995. The diversity of soil communities, the 'poor man's tropical rainforest. Biodivers. Conserv. 5, 135–168.
Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. Ecology 81, 2606–2621.
Gotelli, N.J., McCabe, D.J., 2002. Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. Ecology 83, 2091–2096.
Gotelli, N.J., Hart, E., Ellison, A.M., 2015. EcoSimR: Null Model Analysis for Ecological Data. R Package Version 0.1.0. http://github.com/gotellilab/EcoSimR.
Hörandl, E., 2006. The complex causality of geographical parthenogenesis. New Phytol. 171, 525–538.
Irmler, U., 2006. Climatic and litter fall effects on collembolan and oribatid mite species and communities in a beech wood based on a 7 years investigation. Eur. J. Soil Biol. 42, 51–62.
Karasawa, S., Hijii, N., 2004. Effects of microhabitat diversity and geographical isolation on oribatid mite (Acari: Oribatida) communities in mangrove forests. Pedobiologia 48, 245–255.
Kraft, N.J., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599.
Lebedeva, N.V., Krivolutsky, D.A., 2003. Birds Spread Soil Microarthropods to Arctic Islands 391. pp. 329–332.
Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.
Legendre, P., Legendre, L., 2012. Numerical Ecology. Elsevier, Oxford, UK.
Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecol. Monogr. 75, 435–450.
Lehmitz, R., Russell, D., Hohberg, K., Christian, A., Xylander, W.E., 2011. Wind dispersal of oribatid mites as a mode of migration. Pedobiologia 54, 201–207.
Levin, S., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.
Lindo, Z., Winchester, N.N., 2008. Scale dependent diversity patterns in arboreal and terrestrial oribatid mite (Acari: oribatida) communities. Ecography 31, 53–60.
Lindo, Z., Winchester, N.N., 2009. Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. Oecologia 160, 817–825.
Maaß, S., Maraun, M., Scheu, S., Rillig, M.C., Caruso, T., 2015. Environmental filtering vs. Resource-based niche partitioning in diverse soil animal assemblages. Soil Biol. Biochem. 85, 145–152.
Maraun, M., Martens, H., Migge, S., Theenhaus, A., Scheu, S., 2003. Adding to 'the enigma of soil animal diversity': fungal feeders and saprophagous soil invertebrates prefer similar food substrates. Eur. J. Soil Biol. 39, 85–95.
Maraun, M., Norton, R.A., Ehnes, R.B., Scheu, S., Erdmann, G., 2012. Positive correlation between density and parthenogenetic reproduction in oribatid mites (Acari) supports the structured resource theory of sexual reproduction. Evol. Ecol. Res. 14, 311–323.
Marshall, V.G., Reevrs, R.M., Norton, R.A., 1987. Catalogue of the Oribatida (Acari) of continental United States and Canada. Mem. Entomol. Soc. Canada 119, 1–418.
Martiny, J.B.H., Bohannan, B.J., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., 2006. Microbial biogeography: putting microorganisms on the map. Nat. Rev. Microbiol. 4, 102–112.
Mitchell, R., Urpeth, H., Britton, A., Black, H., Taylor, A., 2016. Relative importance of local- and large-scale drivers of alpine soil microarthropod communities. Oecologia 182, 913–924.
Nielsen, U.N., Osler, G.H.R., van der Wal, R., Campbell, C.D., Burslem, D., 2008. Soil pore volume and the abundance of soil mites in two contrasting habitats. Soil Biol. Biochem. 40, 1538–1541.
Nielsen, U.N., Osler, G.H.R., Campbell, C.D., Burslem, D.F., van der Wal, R., 2010. The influence of vegetation type, soil properties and precipitation on the composition of soil mite and microbial communities at the landscape scale. J. Biogeogr. 37, 1317–1328.
Norton, R.A., 1980. Observations on phoresy by oribatid mites (Acari: oribatei). Int. J. Acarol. 6, 121–130.
Norton, R.A., 1994. Evolutionary aspects of oribatid mite life histories and consequences for the origin of the astigmata. In: Houck, M.A. (Ed.), Mites. Springer, Berlin, pp. 99–135.
Norton, R.A., Behan-Pelletier, V., 1991. Calcium carbonate and calcium oxalate as cuticular hardening agents in oribatid mites (Acari : oribatida). Can. J. Zool. 69, 1504–1511.
Ojala, R., Huhta, V., 2001. Dispersal of microarthropods in forest soil. Pedobiologia 45, 443–450.
Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M.A., 2007. The Vegan Package. Community Ecology Package 10. pp. 631–637.
Patterson, S.L., Zak, D.R., Burton, A.J., Talhelm, A.F., Pregitzer, K.S., 2012. Simulated N deposition negatively impacts sugar maple regeneration in a northern hardwood ecosystem. J. Appl. Ecol. 49, 155–163.
R Core Team, 2016. R: A Language and Environment for Statistical Computing. http://www.r-project.org/.
Reynolds, J.W., 2004. The status of earthworm biogeography, diversity, and taxonomy in North America revisited with glimpses into the future. Earthworm Ecol. 2, 63–74.
Richter, D.D., Markewitz, D., Trumbore, S.E., Wells, C.G., 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400, 56–58.
Rosenberger, M., Maraun, M., Scheu, S., Schaefer, I., 2013. Pre- and post-glacial diversifications shape genetic complexity of soil-living microarthropod species. Pedobiologia 56, 79–87.
Rosindell, J., Hubbell, S.P., He, F., Harmon, L.J., Etienne, R.S., 2012. The case for ecological neutral theory. Trends Ecol. Evol. 27, 203–208.
Saitoh, S., Fujii, S., Takeda, H., 2011. Evaluation of the bottom-up force of accumulated organic matter on microarthropods in a temperate forest floor. Eur. J. Soil Biol. 47, 409–413.
Scheu, S., Parkinson, D., 1994. Effects of invasion of an aspen forest (Canada) by *Dendrobaena octaedra* (Lumbricidae) on plant growth. Ecology 75, 2348–2361.
Schneider, K., Maraun, M., 2009. Top-down control of soil microarthropods – evidence from a laboratory experiment. Soil Biol. Biochem. 41, 170–175.
Siepel, H., 1996. Biodiversity of soil microarthropods: the filtering of species. Biodivers. Conserv. 5, 251–260.
Siepel, H., Ruiter-Dijkman, E.M., 1993. Feeding guilds of oribatid mites based on their carbohydrase activities. Soil Biol. Biochem. 25, 1491–1497.
Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. Oecologia 85, 74–79.
Taylor, A.R., Wolters, V., 2005. Responses of oribatid mite communities to summer drought: the influence of litter type and quality. Soil Biol. Biochem. 37, 2117–2130.
Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proc. Natl. Acad. Sci. U. S. A. 101, 10854–10861.
Vagvolgyi, J., 1975. Body size, aerial dispersal, and origin of the Pacific land snail fauna. Syst. Biol. 24, 465–488.
Van der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N., Cousin, S., Declerck, S., Jeppesen, E., Conde-Porcuna, J.M., Schwenk, K., Zwart, G., Degans, H., 2007. The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. Proc. Natl. Acad. Sci. U. S. A. 104, 20404–20409.
Van Straalen, N.M., Verhoef, H.A., 1997. The development of a bioindicator system for soil acidity based on arthropod pH preferences. J. Appl. Ecol. 34, 217–232.
Wehner, K., Norton, R.A., Blüthgen, N., Heethoff, M., 2016. Specialization of oribatid mites to forest microhabitats–the enigmatic role of litter. Ecosphere 7, e01336.
Weiher, E., Keddy, P.A., 1995. Assembly rules, null models, and trait dispersion : new questions from old patterns. Oikos 74, 159–164.
Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., Bentivenga, S., 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366, 2403–2413.
Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397.
Zaitsev, A.S., van Straalen, N.M., Berg, M.P., 2012. Landscape geological age explains large scale spatial trends in oribatid mite diversity. Landsc. Ecol. 28, 285–296.